

CROWN RATIO INFLUENCES ALLOMETRIC SCALING IN TREES

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Abstract. Allometric theories suggest that the size and shape of organisms follow universal rules, with a tendency toward quarter-power scaling. In woody plants, however, structure is influenced by branch death and shedding, which leads to decreasing crown ratios, accumulation of heartwood, and stem and branch tapering. This paper examines the impacts on allometric scaling of these aspects, which so far have been largely ignored in the scaling theory. Tree structure is described in terms of active and disused pipes arranged as an infinite branching network in the crown, and as a tapering bundle of pipes below the crown. Importantly, crown ratio is allowed to vary independently of crown size, the size of the trunk relative to the crown deriving from empirical results that relate crown base diameter to breast height diameter through crown ratio. The model implies a scaling relationship in the crown which reduces to quarter-power scaling under restrictive assumptions but would generally yield a scaling exponent somewhat less than three-quarters. For the whole tree, the model predicts that scaling between woody mass and foliage depends on crown ratio. Measurements on three boreal tree species are consistent with the model predictions.

Key words: allometry; biomass; branching network; fractal dimension; pipe model; quarter-power scaling.

INTRODUCTION

Woody plants are exceptional among living organisms in that they carry a substantial mass of senescent tissue in their bodies. The trunks and branches of large trees may contain more than half of their weight as heartwood, which takes virtually no part in the metabolic function of the tree (Vanninen et al. 1996, Perez et al. 2004). Retention of senescent tissue would not be evolutionarily stable in most animals, which tend to minimize their energy consumption in movement (Maynard Smith 1982). By contrast, the retention of dead mass appears vital for mechanical support to anchor trees in the ground and to prevent buckling or toppling under strong winds or snow (Greenhill 1881, Mattheck 1998).

It would be surprising if this difference did not have an influence on the evolution of form in woody plants as compared with mobile animals, yet it has been largely ignored by authors who have advanced models of regularities in the form of living organisms (McMahon 1973, Mandelbrot 1983). The most recent unified theory of structure, the quarter-power scaling rules for fractal-like branching networks (West et al. 1997, 1999, Enquist 2002), has stimulated theoretical discussion (Kozłowski and Konarzewski 2004), as well as empirical tests of the predicted allometries (West et al. 1999, Enquist 2002, Meinzer et al. 2005, Pretzsch 2006). However, although recognized in principle (Enquist 2002), consideration of

the effects of branch death and heartwood formation is also absent in the quarter-power scaling model.

A generally accepted theory of heartwood formation does not exist, but a good candidate is provided by the pipe model in its original form (Shinozaki et al. 1964). The pipe model describes trees as bundles of active and disused woody pipes, where the dynamics of the disuse of pipes represents heartwood formation. Related predictions and their implications for stem taper have already been tested in connection with growth models (Mäkelä 2002, Valentine and Mäkelä 2005).

According to the pipe model (Shinozaki et al. 1964), heartwood formation is associated with twig and branch death: as the active woody pipes running from fine roots to foliage lose their connection with foliage they become disused, remaining embedded in the trunk and large branches. Senescence of twigs inside the crown proceeds as foliage expands towards the surface of the crown where light can be more readily captured, leading to the formation of a cavity inside the volume (Horn 1971). Furthermore, as the tops of crowns increase in height, the lower branches may senesce and fall in response to shading by neighbors, leaving a bare trunk. Trunk length does not scale with crown dimensions (Assmann 1970, Holdaway 1986). Nonetheless, the trunk may comprise a considerable part of a tree's mass.

In this paper, we further develop the theory of allometric scaling in woody plants on the basis of the pipe model. The approach draws from West et al. (1999) but with modifications. We define the crown as an infinite branching network, where foliage has a fractal dimension (Mandelbrot 1983). Accounting for disuse of

Manuscript received 15 February 2006; revised 1 June 2006; accepted 5 June 2006. Corresponding Editor: M. J. Lechowicz.

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pipes inside the crown leads to relaxing the assumptions of area-preserving and volume-filling branching (West et al. 1999). For the whole tree, the fractal approach is not directly applicable because the trunk does not scale with the crown dimensions. Following consistent empirical results, we relate the weight of the bare stem to crown weight and crown ratio (Valentine et al. 1994, Kantola and Mäkelä 2004). The predictions of the model are compared with data on three boreal species. Finally, we discuss the general implications of the results.

THE MODEL

Pipe model trees

A pipe model tree has the following properties (Shinozaki et al. 1964):

1) Each unit of leaf is attached to an active pipe of unit cross-sectional area and zero taper that runs from the petiole to a unit of fine root through a network of branches, stem, and woody roots. In aggregate, a bundle of active pipes is area preserving.

2) Following branch and twig death and shedding, some pipes turn into *disused pipes* that lose their connection to the foliage, stop growing and become embedded in the woody structure. The bundle of active and disused pipes tapers.

3) Inside the crown, disused pipes are formed as foliage expands towards the surface of the crown, shading the inner part. This leads to the formation of a *cavity* inside the crown envelope.

4) Below the live crown, whole branches become detached from the foliage as the tree grows. This process leads to the self-pruning of the crowns and results in the formation of the bare trunk and the phenomenon of “crown rise.” The disused pipes remain in the bare trunk, giving it the characteristic taper.

In order to investigate the allometric scaling in the pipe model trees, we apply a fractal approach (Mandelbrot 1983) resembling the fractal-like scaling model by West et al. (1999). However, the below-crown trunk cannot be included in the fractal analysis because in fractals, the length of the first internode, i.e., the trunk, should be proportional to total length, i.e., tree height. This cannot be expected in real trees where crown ratio largely depends on tree age and the history of population density during the tree's life-time (Assman 1970). Our analysis is therefore cast in two phases starting with the crown only, then extending to the trunk.

Scaling in fractal crowns

The fractal model describes a tree with $N \rightarrow \infty$ branching levels, starting from the trunk (level 0) and ramifying into n identical daughter branches at each branching level k . The length of a branching unit or internode, l_k , decreases at each level by the factor γ , hence $l_{k+1} = \gamma l_k$. The diameter of the branching unit at level k is r_k . The consecutive diameters follow the rule $r_{k+1} = n^{-a/2} r_k$ where $a \geq 1$. In addition, the diameter of

individual active pipes, a_k , is conserved from one level to the next: $a_{k+1} = a_k$. Finally, internodal length scales with internodal diameter as $l_k \propto r_k^\alpha$ (see Appendix A for a list of symbols).

The branch tips of this branching system define a fractal with dimension z , related to γ and n as $\gamma = n^{-1/z}$ (Mandelbrot 1983). Branch tips are identified with a unit foliage, their assemblage representing total foliage mass, M_F . Foliage mass therefore scales with total length, L_0 , as $M_F \propto L_0^z$ (Appendix B).

It can be shown that, in this fractal crown, woody mass scales as $M \propto L_0^{(2/\alpha+1)}$, and further, that $\alpha = 2/z$ (Appendix C). This leads to the following scaling rule:

$$M_F \propto M^{z/(z\alpha+1)}. \quad (1)$$

Clearly, if $a = 1$ and $z = 3$, the result reduces to the quarter-power scaling proposed by West et al. (1997, 1999). In the pipe model tree, however, (1) $a > 1$ because of twig senescence, and (2) $z < 3$ because of the cavity created inside the crown as a result of twig senescence. The presence of heartwood inside the crown is well documented (Vanninen et al. 1996, Meinzer et al. 2005, Longetaud et al. 2006), but we are not aware of any studies that have quantified the taper parameter a . By contrast, there is ample empirical evidence concerning the fractal dimension z (e.g., Zeide and Pfeifer 1991, Mäkelä and Sievänen 1992, Ilomäki et al. 2003).

Scaling in whole trees with variable crown ratios

As noted earlier, the fractal approach does not apply to the trunk below the live crown, because the length of the trunk does not scale with that of the crown. Instead, crown ratio, r_C , may vary according to the growth history of the tree. Crown ratio is defined by $H_C = r_C H$, where H_C is crown length and H is tree height. Generally, $H_C \propto L_0$ with $H_C \leq L_0$ because of the branching angle. Here, we shall assume for simplicity that $H_C = L_0$, a condition only strictly true in species with monopodial growth.

The trunk tapers because of the variable length of the disused pipes embedded in it. Denote the basal area of the stem at crown base by A , and that at the stem base by B . A key assumption in our derivation of a scaling rule for the whole tree is one based on empirical observation, suggesting that the tapering of the trunk can be approximated with the crown ratio (Valentine et al. 1994):

$$A = r_C B. \quad (2)$$

This result appears to have no direct theoretical basis, however, it is approximately consistent with both stem form as projected by the theory of constant strain (Morgan and Cannell 1994) and the dynamic development of trees according to the pipe model, given realistic patterns of crown rise (Mäkelä 2002, Valentine and Mäkelä 2005).

Using Eq. 2, we show in Appendix D that in a tree with a fractal crown, foliage scales with total above-ground woody mass, M_T , approximately as

$$M_F \propto (r_C^2 M_T)^{z/(az+1)}. \quad (3)$$

The scaling relationship is accurate if average (active + disused) pipe length inside the crown is $0.5(L_0)$ (Appendix D). This result has the significant implication that the allometric relationship between wood and foliage should depend on how crown ratio is distributed in the data set. If crown ratio increases with increasing foliage mass, the allometric exponents should appear larger than $z/(az+1)$. By contrast, if crown ratio decreases with increasing foliage mass, the allometric exponents should appear smaller than $z/(az+1)$.

In the following sections, we set out to test these scaling predictions against empirical data.

MATERIAL AND METHODS

In order to test the model predictions (Eqs. 1 and 3), biomass data for foliage, wood in the crown, and wood below crown, are needed. For a stringent test of Eq. 4, both cross-sectional and longitudinal data sets are required. Such measurements are not standard in forest research. However, a few studies have recently been conducted that lend themselves ideally for our purpose.

The data sets comprise biomass and dimensional measurements on Norway spruce (*Picea abies* (L) Karst.) (Kantola and Mäkelä 2004), Scots pine (*Pinus sylvestris* (L.)) (Vanninen et al. 1996, Vanninen and Mäkelä 2000), and silver birch (*Betula pendula* Roth.) (Parviainen 1999, Ilomäki et al. 2003). In all data sets, the same measurement procedure was used to determine biomass of foliage, branches, and stems. The woody biomass can be further divided into within-crown and below-crown components (except in Parviainen 1999). In addition, tree height, crown length, diameter at breast height, and diameter at crown base were measured. Crown base was defined as the base of the continuous crown, with no more than two consecutive internodes without live branches.

Norway spruce.—29 trees were sampled from three permanent experimental sites in southern Finland, aged 25, 67, and 86 years (Kantola and Mäkelä 2004). The two older sites were further divided into three plots that had undergone different thinning treatments: control (five sample trees each), normal thinning (four sample trees each), and heavy thinning (three sample trees each). Five sample trees came from the unthinned, young plot. Trees were selected to include trees from all dominance classes.

Scots pine.—In the cross-sectional data set, data came from a 44-year-old stand in southern Finland with one dense and one sparse plot, including 11 sample trees (Vanninen and Mäkelä 2000). Trees from all dominance classes were selected. (One heavily suppressed tree was discarded as an outlier because its foliage mass was clearly declining.) In the longitudinal data set, 18

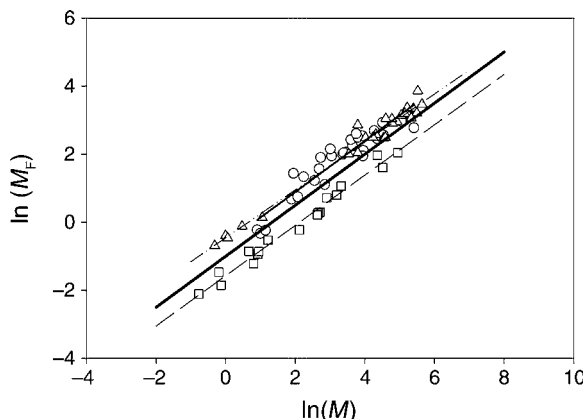


FIG. 1. Scaling between woody mass (M ; kg) and foliage mass (M_F ; kg) inside the crown. M includes live branches and stem above crown base (defined as the base of the continuous crown, with no more than two consecutive internodes without live branches). Key to symbols: circles and solid black line, pine (*Pinus sylvestris*); triangles and dashed line with dots, spruce (*Picea abies*); squares and long dashed line, birch (*Betula pendula*). The lines are linear least-squares fits to the log-transformed data, $x = \ln(M)$, $y = \ln(M_F)$: pine, $y = 0.7510x - 0.6105$, $R^2 = 0.88$, $N = 29$; spruce, $y = 0.7041x - 0.4569$, $R^2 = 0.98$, $N = 29$; birch, $y = 0.7392x - 1.5709$, $R^2 = 0.98$, $N = 18$. The heavy black line represents the 3/4 power law ($y = 0.75x - 1.0$).

dominant trees were sampled to include a wide age range from 20 to 250 years (Vanninen et al. 1996). Two site types, fertile and barren, were included.

Silver birch.—The cross-sectional data set comes from a 29-year-old stocking experiment in southern Finland, including 18 sample trees from a dense (planting density 5000 trees/ha), medium (1600 trees/ha), and sparse (400 trees/ha) plot (Ilomäki et al. 2003). Trees from all dominance classes were sampled. The longitudinal data set consists of 12 dominant trees from seven sites, with heights ranging from 1.8 m to 27.8 m and ages from three to 74 years (Parviainen 1999). This data set does not separate stem within and below crown.

Statistical methods.—The scaling exponents of Eqs. 1 and 3 were determined from a linear regression of the log-transformed equations. A one-tailed t test was applied to compare the exponent with the value 0.75 predicted by the quarter-power law.

RESULTS

The scaling exponent between foliage and woody mass in crowns (Eq. 1) was estimated to vary between 0.70 and 0.75 in our data set consisting of *Betula pendula*, *Pinus sylvestris*, and *Picea abies* (Fig. 1). These values suggest that, assuming $z < 3$, a could be very slightly larger than 1. However, the scaling exponents are not statistically significantly smaller from the prediction by the quarter-power scaling model, which suggests the value of 3/4 for the exponent (West et al. 1997, 1999, Enquist 2002; $P = 0.49$, $P = 0.33$, and $P = 0.015$ for pine, birch, and spruce, respectively). The

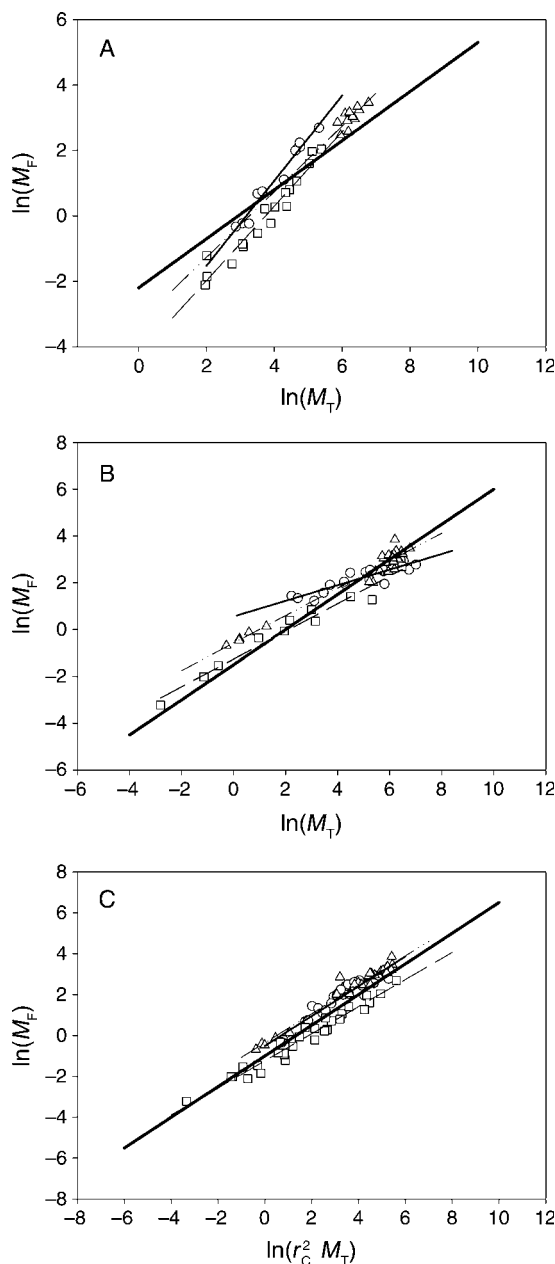


FIG. 2. Scaling between aboveground woody mass (M_T ; kg) and foliage mass (M_F ; kg) in the tree. M_T includes live branches and the trunk. Key to symbols: circles and solid black line, pine (*Pinus sylvestris*); triangles and dashed line with dots, spruce (*Picea abies*); squares and long dashed line, birch (*Betula pendula*). The lines are linear least-squares fits to the log-transformed data. The heavy black line represents the 3/4 power law ($y = 0.75x + C$, where C is an appropriate number to bring the line level with the data). (A) For each species, data include trees of different dominance position in one even-aged stand; $x = \ln(M_T)$, $y = \ln(M_F)$: pine, $y = 1.3011x - 4.1278$, $R^2 = 0.96$, $N = 10$; spruce, $y = 1.0028x - 3.2726$, $R^2 = 0.77$, $N = 12$; birch, $y = 1.1381x - 4.2599$, $R^2 = 0.95$, $N = 18$. (B) Data include dominant (and other for spruce) trees from stands of variable age; $x = \ln(M_T)$, $y = \ln(M_F)$: pine, $y = 0.3338x + 0.5592$, $R^2 = 0.81$, $N = 18$; spruce, $y = 0.5868x - 0.5772$, $R^2 = 0.95$, $N = 29$; birch, $y = 0.55908x - 1.2595$, $R^2 = 0.97$, $N = 12$. (C) All data are pooled to

scaling model accounts for 88–98% of the variation in the log-transformed data.

To test the predictions of Eq. 3, we first analysed the whole-tree allometry separately for the cross-sectional and longitudinal data sets. In the cross-sectional data sets, all trees came from the same even-aged stands, suggesting that any variation in crown ratio was caused by competition. Larger trees then tend to have larger crown ratios (Holdaway 1986, Hasenauer and Monserud 1996). In this case, when M_F was regressed directly against M_T without accounting for r_C , the allometric exponent appeared considerably larger than $z/(az + 1)$, as determined by the crown analysis (Fig. 2A). The exponents were statistically significantly larger than 0.75 for pine and birch ($P < 0.001$) but not for spruce ($P = 0.088$).

By contrast, observations of mean or dominant trees from stands of different ages tend to show decreasing crown ratios with increasing tree size (Holdaway 1986, Mäkelä and Vanninen 1998). Indeed, the allometric exponents appeared smaller than $z/(az + 1)$ when the longitudinal data was analysed without accounting for crown ratio (Fig. 2B). All exponents were statistically significantly smaller than 0.75 ($P < 0.001$). However, including crown ratio as suggested by Eq. 3 caused both types of data to fall about the same line, with scaling exponents similar to those in the crown, as predicted by Eq. 1 (Fig. 2C). The exponents for spruce and pine were not statistically significantly smaller than 0.75 ($P = 0.056$ and $P = 0.33$, respectively), but the exponent for birch was ($P < 0.001$).

DISCUSSION

Our analysis has shown that crown ratio influences the allometric scaling between foliage and woody mass in trees. Because crown ratio varies, largely according to the growth history of the tree, universal scaling exponents cannot be defined for trees. This kind of size-dependent allometry has been pointed out previously (e.g., Niklas 1995, Chambers et al. 2001, Niklas and Spatz 2004), however, we have for the first time been able to attribute the size dependence to crown ratio.

The pipe model provides a conceptual framework for incorporating the dynamic processes that lead to crown rise and the related changes in allometry. The disuse of pipes following branch death is the central driver in this development. The key assumption used in the derivation, Eq. 2, was an empirical one and did not appear to follow directly from any general analysis. In the pipe model, the shape of the trunk is determined largely by the rate of crown rise relative to height growth, which in

fit $y = \ln(M_F)$ against $x = \ln(r_C^2 M_T)$: pine, $y = 0.7283x - 0.5074$, $R^2 = 0.86$, $N = 29$; spruce, $y = 0.7081x - 0.3569$, $R^2 = 0.96$, $N = 29$; birch, $y = 0.6623x - 1.2402$, $R^2 = 0.96$, $N = 30$.

turn depends on the competitive status of the tree (Mäkelä 2002, Valentine and Mäkelä 2005). It is possible to show analytically that if crown rise is proportional to height growth at all times, then Eq. 2 follows in a pipe model tree. The same is approximately true of trees that follow this strategy approximately, which indeed seems to be the case in real trees (Valentine and Mäkelä 2005). Mäkelä (2002) demonstrated that the stem shape in such trees is also in agreement with the theory of constant strain (Morgan and Cannell 1994), and that both approaches produce realistic stem shapes (Mäkelä 2002).

That “the largest trees may ... deviate from ... allometric scaling relations due to the shedding of terminal branches associated with senescence” has already been recognized as a need to “add subtle detail” to the quarter-power scaling model (Enquist 2002). Our model adds detail in terms of crown ratio, and our analysis suggests that this detail is appropriate for trees of any size, not just the largest trees. Crown rise starts at canopy closure, which largely depends on stand density. In managed boreal forests, for example, it occurs around the age of 20 years at less than 30% of maximum tree height (Hynynen 1995). The increasing proportion of disused pipe area with increasing stem diameter below the crown also explains why the area-specific conductivity should decrease with increasing cross-sectional area at breast height (Meinzer et al. 2005), contrary to the prediction by the quarter-power scaling model (Enquist 2002).

Inside the crown, the consequences of the disuse of pipes were of less significance in our data, which suggested that the taper parameter a could only be slightly larger than 1. However, it seems plausible to assume that some trees show stronger tapering of heartwood than others. For example, old conifers with large crowns but little crown rise should have a considerable heartwood content at the base of the crown, whereas the crowns of younger, fast growing trees primarily consist of sapwood (Vanninen et al. 1996, Longetaud et al. 2005). An interesting consequence of our derivation is that because $z = 2/\alpha a$, crowns with larger heartwood taper should develop sparser crowns, provided that the height-diameter scaling exponent α remains constant. Empirical observation supports this finding in Scots pine, where z was smaller in old than young trees (Mäkelä and Vanninen 1998).

Our model of crown structure was stimulated by the well-known scaling model by West et al. (1997, 1999, Enquist 2002), though the present formulation uses a proper fractal, rather than a finite fractal-like branching network with terminal internodes of fixed length. It turns out that the fractal-like model of West et al. (1999) approaches quarter-power scaling asymptotically, though for practical purposes, convergence is achieved within 20 branching levels. A fractal-like model affords the investigation of sap flow through tapering vascular tubes (West et al. 1999, Enquist 2002, Mäkelä and

Valentine 2006), but we do not require vascular tubes, tapering or otherwise, to investigate the effect of crown ratio on allometric scaling. Besides, the pipe model with its area-preserving unit pipes was intended to be a conceptual model of stem form in trees (Shinozaki et al. 1964); it was never intended to be a structural or functional model of vascular vessels or tracheal elements.

As a result, our fractal model is not concerned with water relations, but with scaling of size only. The assumptions about active pipe properties (e.g., Enquist 2002) are hence largely irrelevant for our results, which rely on the properties of the bundles of active and disused pipes only. In fact, our fractal model is therefore an application of the model originally proposed by Mandelbrot for trees following area-preserving branching (Mandelbrot 1983). However, the recent results by Meinzer et al. (2005) suggest that simply accounting for disused pipes may provide a more adequate first approximation of mean conductivity properties than the derivations of the quarter-power scaling model that ignore the disuse of pipes.

The significance of crown ratio in the biomass relations and form of trees has already been pointed out previously in studies applying the pipe model (e.g., Mäkelä and Vanninen 1998, Ilomäki et al. 2003, Valentine and Mäkelä 2005). The added value of the fractal approach is that it actually allows us to derive the allometric scaling exponents between wood and foliage (Eqs. 1 and 3). However, this requires some simplifying assumptions that have been avoided in previous pipe model derivations. For example, all active pipes have equal length in the fractal model, while average pipe length is an empirical parameter in the pipe model approach (e.g., Valentine and Mäkelä 2005). This turned out to be critical for deriving Eq. 3, where the empirical instead of theoretical pipe length had to be used for consistency (Appendix D).

Our analysis has shown that the dynamics of disused pipes and especially the phenomenon of crown rise are of primary importance for scaling between woody mass and foliage in trees. In addition of their theoretical interest, these results could have practical value, e.g., for developing operational methods to estimate carbon budgets in forested areas. These results promote the inclusion of crown ratio as a standard measure in forest inventories, as well as suggest that stronger efforts should be taken to improve the quantitative models of branch senescence and crown rise.

ACKNOWLEDGMENTS

We thank P. Vanninen and A. Kantola for making data available for this study. A. Mäkelä was supported by the Academy of Finland, grant no. 206307.

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APPENDIX A

Complete list of symbols used in the model (*Ecological Archives* E087-176-A1).

APPENDIX B

Greenhill scaling and fractal dimension in the branching network (*Ecological Archives* E087-176-A2).

APPENDIX C

Scaling in the crown (*Ecological Archives* E087-176-A3).

APPENDIX D

Scaling in the whole tree (*Ecological Archives* E087-176-A4).